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Oldest southern sauropterygian reveals early marine reptile globalization

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Sauropterygians were the stratigraphically longest-ranging clade of Mesozoic marine reptiles with a global fossil record spanning ~180 million years[1]. However, their early evolution has only been known from what is now the Northern Hemisphere, extending across the northern and trans-equatorial western margins of the Tethys paleo-ocean[1] after the late-Early Triassic (late Olenekian, ~248.8 million years [Ma] ago[2]), and via possible trans-Arctic migration[1] to the Eastern Panthalassa super-ocean prior to the earliest Middle Triassic (Olenekian–earliest Anisian[3,4], ~247 Ma). Here, we describe the geologically oldest sea-going reptile from the Southern Hemisphere — a nothosaur (basal sauropterygian[5]) from the Middle Triassic (Anisian, after ~246 Ma[6]) of New Zealand. Time-scaled ancestral range estimations thus reveal an unexpected circum-Gondwanan high-paleolatitude (>60° S[7]) dispersal from a northern Tethyan origination center. This coincides with the adaptive diversification of sauropterygians after the end-Permian mass extinction[8] and suggests that rapid globalization accompanied their initial radiation in the earliest Mesozoic.

The nothosaur fossil (New Zealand National Paleontological Collection, GNS Science [GNS] CD 540: Figures 1A and S1A–D) was recovered from a loose boulder found along the main tributary of Balmacaan Stream at the base of Mt Harper in the Harper Range on central South Island, New Zealand[9]. The encasing indurated siltstone rock conforms to adjacent strata of the Balmacaan Formation, which has produced a rich macroinvertebrate fauna, including the lophospirid gastropod *Mellarium*[9] that occurs in direct association with GNS CD 540 (Figure S1E) and is age-diagnostic for the lower Etalian stage of the New Zealand Geological Timescale[6] (= mid-lower to upper Anisian). We also extracted inertinite (degraded plant material) as the dominant organic component in the adhering siltstone; this accords with abundant woody plant remains and regressive nearshore depositional conditions reported for the Balmacaan Formation[9].

GNS CD 540 is an isolated posterior-most dorsal vertebra that has been weathered by water transport, destroying the prezygapophyses, leading edge of the neural spine, and anterior articular surface of the centrum. Nonetheless, the well preserved posterior articular surface is flat, indicating an originally platycoelous centrum profile, and together with weakly constricted centrum sides, laterally expanded centrum-neural arch contact, short transverse processes (accommodating most of the dorsal rib facet), and inset zygantrum situated between the shallowly inclined (~20º) postzygapophyses, denotes morphological compatibility with Eosauropterygia (the clade incorporating pachypleurosaurs, nothosaurs, pistosaurs and plesiosaurs)[5]. The absence of pachyostotic internal bone structure, accessory infrapostzygapophyses, and the retention of zygosphene–zygantrum

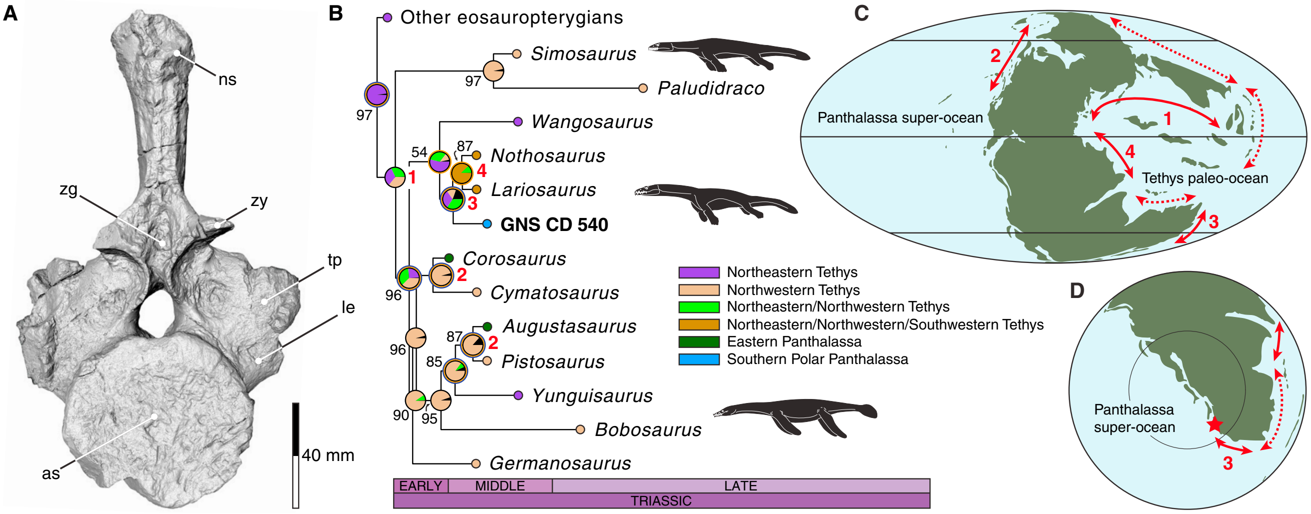

Figure 1. Morphology and biogeographic context of the oldest Southern Hemisphere sauropterygian.
(A) mCT image of the GNS CD 540 dorsal vertebra in posterior view. (B) Time-scaled[8] Bayesian phylogeny (Figure S1G) of Nothosauroidea (silhouettes) with estimated ancestral ranges (pie charts), dispersal (orange circles) and vicariance (blue circles) events (Table S1). Node numbers indicate geographic ranges (red) and percent (>50%) support (black) for ancestral range estimations. (C) Middle Triassic global map showing ancestral ranges (solid arrows) and possible dispersal routes (dashed arrows; modified from maps compiled by Colorado Plateau Geosystems Inc. https://deeptimemaps.com/). (D) Middle Triassic southern polar map with occurrence of GNS CD 540 (red star). Anatomical abbreviations: as, centrum articular surface; le, laterally expanded neural arch contact; ns, neural spine; tp, transverse process; zg, zygantrum; zy, postzygapophysis. Geographic ranges: (1) Northeastern to Northwestern Tethys; (2) Northwestern Tethys to Eastern Panthalassa; (3) Northern Tethys to Southern Polar Panthalassa; (4) Northern Tethys to Southwestern Tethys.

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articulations differentiates GNS CD 540 from pachypleurosaurs, pistosaurs and plesiosaurs[5], respectively. Finally, the large size (maximum vertebral height/centrum diameter = 123.6/53 mm) and tall neural spine with transversely expanded apex are particularly reminiscent of *Nothosaurus* species described from Middle Triassic (Anisian–Ladinian) Gondwanan shelf deposits in the Middle East[5].

We scored GNS CD 540 into a published tip-dated phylogeny of sauropterygians[8] to timescale our ancestral range estimations and reconstruct a dispersal history for the group. These analyses (Supplemental information) unanimously placed GNS CD 540 in the monophyletic clade Nothosauroidea (Figures 1B and S1F,G), comprising nothosaurs with closely related simosaurids and pistosauroids (pistosaurs and plesiosaurs)[5]. While species-level geographic sampling of the parent dataset is incomplete, we retrieved a robustly supported origination center from the northeastern Tethys (Figure 1C) that coincides with the inferred emergence of nothosauroids around the earliest Triassic[8]. A subsequent range expansion into the northwestern Tethys accompanied nothosauroid intra-clade divergences across the mid-Early Triassic[8], and likely facilitated the southward radiation of nothosaurs (as well as simosaurids, pistosauroids and other sauropterygians[5]) along the contiguous shallow marine shelf of northern Gondwana during the Middle Triassic[5]. Significantly, we now also show that nothosaurs achieved an extended extra-Tethyan dispersal circumscribing the entire peninsular landmass of eastern Gondwana to reach the Panthalassan southern polar periphery by at least the early-Middle Triassic (Figure 1D). An opposing southeastern Tethyan migration route (perhaps following island chains to cross open ocean) might have been feasible but contrasts with the restricted coastal habitats assumed for most Triassic sauropterygians[1,4,5,10].

In summary, the discovery of GNS CD 540 pushes back the fossil record of Southern Hemisphere sauropterygians by over 40 Ma[10], and demonstrates that previously equivocal Austral Triassic occurrences are clearly a result of insufficient sampling[10]. Furthermore, the unambiguous high-paleolatitude setting of GNS CD 540 counters the proposal that adverse paleoenvironments prevented Triassic sauropterygians from poleward dispersals[5], which otherwise explains their unusually disjunct distribution bridging the peri-equatorial northern Tethyan to Eastern Panthalassan oceans[1]. Indeed, isotopic paleotemperatures provide no indication of cold climate barriers[7] hindering marine reptile migrations across Triassic high-paleolatitudes. We therefore expect future exploration to yield more Triassic sauropterygian fossils from the Southern Hemisphere, highlighting the importance of GNS CD 540 as the first evidence of early globalization concurrent with the establishment of complex marine tetrapod ecosystems, and the rise of reptiles as oceanic predators after the end-Permian mass extinction[4].

SUPPLEMENTAL INFORMATION

Supplemental information including one figure, a table and methods can be found with this article online at https://doi.org/10.1016/j.cub.2024.03.035.

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AUTHOR CONTRIBUTIONS

B.P.K. conceived and designed the study, analysed the data, interpreted the results, and wrote the manuscript. A.J.R. and J.H.H. contributed fossil preparation, μCT scans, segmentation, and rendering. G.Y. and M.T. organized specimen access and export permits. D.J.M. and I.S.B. processed and interpreted the microfossil samples. All authors were involved in discussing the results and revising the manuscript.

DECLARATION OF INTERESTS

The authors declare no competing interests.

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